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IBP

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ABSTRACT

Estimates of the standing crop biomass and dry matter per hectare for the desert environment of Deep Canyon, California, are included. Primary productivity rates based on periodic growth measurements for the three species are presented. The rates are lower than other recorded rates of net primary production in a desert environment.

CO_2 assimilation by *Opuntia basilaris* has been restricted to periods following rainfall, with negligible rates of fixation during the hours of daylight in all cases. Dark CO_2 assimilation is relatively low (.5 - 1 mg $CO_2/dm^2/hr$) with near ambient concentrations of carbon dioxide. CO_2 assimilation is increased with increasing concentrations of carbon dioxide, the effects of which are linear up to 1000 ppm CO_2. During periods immediately following rainfall the magnitude of exogenous CO_2 assimilation is increased, which appears to yield more favorable water-use efficiency ratios.

Estimates of dark CO_2 assimilation and subsequent photosynthetic carbon assimilation based on the diurnal fluctuation of total acids are presented. These estimates are 1 to 1.5 times the rates of CO_2 assimilation yet recorded for *O. basilaris*.

Transpirational loses of water vapor are also restricted to periods immediately following rainfall. The minimum gas diffusion resistances for *O. basilaris* are approximately 25 sec/cm, which yield calculated transpiration rates of approximately .3 - .4 grams $H_2O/dm^2/hr$. The stomata appear to be more controlled by environmental parameters (i.e., light and temperature) than by plant water status.

Plant water status is directly regulated by the availability of soil water. Increases in plant water status by absorption of soil water has not been demonstrated at soil water potentials below -40 Bars. The *Opuntia* plants appear to show maximum rates of absorption during the daylight hours.

INTRODUCTION

This report contains the observations that have been made during the past year on the productivity and gas exchange characteristics of 3 species of *Opuntia*. The results presented below are only preliminary to obtaining a satisfactory understanding of how environmental factors interact with the processes of primary and biomass production. The study is being continued.

The genus *Opuntia* is well represented in the deserts of the western hemisphere. There are approximately 300 species extending from Canada to the tip of South America. Many of them appear as dominants in the vegetation complexes of the desert regions. The three species reported on here, *O. basilaris*, *O. bigelovii*, and *O. acanthocarpa*, are particularly conspicuous components of the vegetation in the Sonoran and Colorado deserts of the southwestern United States and Northern Mexico. Perhaps the most distinctive feature of the genus is its succulent habit. This feature is common to the whole family Cactaceae to which *Opuntia* belongs. It is also an important characteristic of many other desert species belonging to other families not only in the Sonoran and Colorado deserts but in other warm deserts of the world. Together such succulents often comprise a very substantial part of the vegetation responsible for the primary production of desert ecosystems. There is considerable evidence in the literature to suggest that the succulent habit is correlated with a very special type of production physiology.

It has become apparent through our observations with *Opuntia* that the usual near one-to-one relationship between energy fixation and the assimilation of exogenous CO_2 does not, in all probability, hold for succulents. It appears that once atmospheric CO_2 is incorporated into succulent tissue it may be retained and recycled through respiration, dark fixation and photosynthesis. In such a system a single molecule of CO_2 might be utilized in the production of high energy chemical bonds over and over again without becoming involved in exogenous gas exchange. This observation may be very important to an understanding of the functions of other components, i.e., trophic levels of desert ecosystems in which succulents provide a major part of the primary production potential.

OBJECTIVES

1. To determine the relationship among water status, temperature, gaseous exchange, and vegetative growth of *Opuntia* species under field conditions.

2. In addition to the original objectives; to estimate biomass production rates and standing crop biomass in the desert environment.

3. Use the data obtained in developing a predictive model for estimating productivity for periods encompassing the range of environmental conditions to which the species is naturally subjected but for which observations will not have been made.

4. To gain further insight into fundamental functions which help to determine the success of succulents in arid environments. In this respect the genus *Opuntia* represents one of the most successful plant taxa in the Western hemisphere.

METHODS

Biomass (DSCODE A3UTM10)

Number of joints per plant obtained by direct counting. Fresh weights obtained by weighing joints of various sizes. Dry weights obtained by weighing joints of various sizes, which have been oven-dried for 48 hours at 90°C. Whole plants of various sizes weighed in the field to establish a size vs. field weight correlation. Standing crop biomass estimated by correlating the whole plant size to whole plant weight estimates.

Productivity (DSCODE A3UTM11)

Length of joints obtained by direct measuring. Width (or diameter) of joints obtained by direct measuring. Changes in linear dimensions due to growth obtained by periodic re-measurements of marked joints. Changes in joint weights due to growth estimated from size vs. weight correlations.

CO_2 Assimilation (DSCODE A3UTM20)

CO_2 assimilation by methods of Austin and Longden (1967), and Shimshi (1969). Analyses of CO_2 assimilation are performed at various time periods throughout the entire day, and are repeated with different concentrations of CO_2. Half-maximum CO_2 concentration obtained for the rate of CO_2 assimilation at half the maximum CO_2 assimilation rate (Gates et al., 1969).

Total Acid Number (DSCODE A3UTM21)

Total acid number by modified method of Sideris, Young and Chun (1948). Tissue sections are harvested at various time periods throughout the entire day and are stored under dry ice. Approximately five grams fresh weight of tissue are homogenized in distilled water, filtered, and titrated to pH 6.5 with 0.01 N NaOH to determine total acid number. The pH of the homogenate is read directly from a pH meter prior to titrations.

Gas Diffusion Resistance and Transpiration (DSCODE A3UTM30)

Gas diffusion resistance by methods of Ting, Thompson and Dugger (1967), with a van Bavel type diffusion resistance hygrometer. Diffusion resistances determined from transit time of .2 to .3 on the microamp scale of the diffusion resistance hygrometer. Calibration of the diffusion resistance hygrometer by method using discs which lose water vapor at a known constant rate.

Tissue temperature by direct measuring with thermocouple, infrared thermometer, or thermister. Air temperature by direct measuring with thermocouple. Relative humidity by direct measuring with a portable, electric hygrometer.

Water Status Estimates (DSCODE A3UTM40)

Thermocouple psychrometer probes are inserted into the joint and allowed to equilibrate. The water potential of the tissue can then be directly measured with a thermocouple psychrometer.

Respiration (DSCODE A3UTM50)

Net CO_2 exchange by use of an open-system infrared gas analyzer, and/or O_2 consumption by use of manometer or oxygen polarigraph.

Soil Water Status (DSCODE A3UTM60)

Soil psychrometer probes are placed at different soil depths and allowed to equilibrate. Soil water potential determined directly using a thermocouple psychrometer.

FINDINGS

Biomass (DSCODE A3UTM10)

The two study sites were surveyed during September, 1971, and data for standing crop biomass, cover, density, and floristic composition were collected. Circular plots with an area of 100 square meters were chosen randomly within the study sites to obtain the vegetation data presented in Table 1. All of the data are based on an area of 1 hectare, although we did not sample more than 1/10 of a hectare at each study site. A partial summary of the vegetation analysis data is presented in Table 2.

Table 1. Comparison of the vegetation for the two study sites. Cover, density and standing crop biomass (field weights) were determined only for those plant species located within the boundaries of the study sites.

	Site 01			Site 02		
	(M^2) cover	(ha) density	(KG) biomass	(M^2) cover	(ha) density	(KG) biomass
Cactaceae						
Echinocactus acanthodes	1.0	15	940	3.30	25	90.70
Echinocereus engelmanii	3.0	20	172	22.20	90	378.00
Mammillaria dioica	14.5	720	194	0.02	20	3.25
Opuntia acanthocarpa	137.4	490	2580	243.00	700	349.00
O. basilaris	13.4	160	360	33.40	50	172.50
O. bigelovii	51.2	1000	1586	66.80	1175	2385.00
O. ramossissima	52.4	250	968	0.0	0	0.0
Agavaceae						
Agave deserti	0.0	0	0	498.7	60(170)*	11275.00
Asteraceae						
Bebbia juncea	0.0	0	0	15.25	25	85.00
Encelia farinosa	154.5	140	296	378.70	1000	671.20
Franseria dumosa	90.8	150	40	1166.00	1650	2257.00
Hymernoclea salsola	99.0	260	101	39.70	25	22.50
Euphorbiaceae						
Ditaxis lanceolata	36.0	190	98	79.40	375	133.50
Euphorbia polycarpa	6.6	1060	48	6.85	1225	55.50
Lamiaceae						
Hyptis emoryi	8.9	60	37	0.0	0	0.0
Salvia vaseyi	0.0	0	0	42.0	25	136.20
Fabaceae						
Acacia greggii	0.0	0	0	31.4	50	158.70
Dalea schottii	291.1	90	280	108.2	25	85.00
Zygophyllaceae						
Larrea divaricata	175.7	150	150	0.0	0	0.0
Polygonaceae						
Eriogonum inflatum	5.8	30	9	26.0	200	18.80
Ephedraceae						
Ephedra aspera	0.0	0	0	21.0	50	68.00
Poaceae						
Hilaria rigida	0.7	10	1	487.0	2925	641.20

*Sixty individual plants, 10 of which were rosettes, composed of 170 vegetative members.

Table 2. Partial summary of the vegetation data presented in Table 1. Total succulent standing crop biomass and percent succulent biomass determined from the members of both the Agavaceae and Cactaceae.

	Site 01	Site 02
Total cover (M^2)	1071.0	3269.0
% cover/hectare	10.7	32.6
Total standing crop biomass (Kg)	7864.0	22458.0
Total succulent standing crop biomass	6802.0	18143.0
% succulent biomass	86.5	80.7

Standing crop biomass has been determined in terms of field weights and does not indicate the dry matter composition of the vegetation at the two study sites. Percentage dry matter determinations have been conducted for some of the species included in the vegetation analysis. The results available at present are listed in Table 3.

Table 3. Comparison of the dry matter component for the vegetation at the two study sites. Dry matter values obtained by multiplying the estimated standing crop biomass by the percent dry matter fraction for each plant species.

Species	Site 01	Site 02
Opuntia acanthocarpa	1500.0	140
Opuntia basilaris	95.0	40
Opuntia bigelovii	580.0	880
Bebbia juncea	0.0	35
Encelia farinosa	150.0	340
Franseria dumosa	23.0	1220
Ditaxis lanceolata	68.0	93
Hyptis emoryi	20.0	0
Acacia greggii	0.0	82
Larrea divaricata	93.0	0
Hilaria rigida	0.9	620

1. Determinations of percent dry weight provided by Turner (1972).

The survey of dry matter determinations suggests that seasonal changes occur in the percentage dry weight for the nonsucculent species, although a similar trend is not evident in the succulent species at the two study sites. There does, however, appear to be a difference in percentage dry matter for the *Opuntia* species from the two sites. Site 01, at an elevation of 925 feet, has a consistently lower percentage dry weight per unit field weight than does Site 02, which is located at an elevation of 2,575 feet.

Productivity (DSCODE A3UTM11)

During the period from May, 1971, through December, 1971, growth in the three *Opuntia* species has been followed by measuring changes in linear dimensions. Photographic records of the individual plants have proven to be the best tool for identifying the distinct stem sections to be measured without disturbing the growth or causing injury. Periodic measurements of the length, width, and thickness for *O. basilaris*, and of lengths and diameters for *O. acanthocarpa* and *O. bigelovii* have proven to be very time-consuming and often yielded nonsense growth patterns. In addition, we have collected sufficient information relating measurements of length to width, length to diameter, length to surface area, and length to volume, to accurately estimate growth changes from the changes in length of the individual stem sections.

The three species were initially grouped into three age classes -- juvenile, young and mature -- so that differences in productivity for plants of different ages could be detected. At each site three representative plants of each species were selected from each age class for the periodic growth measurements. During the study period, growth measurements were taken on 330 stem sections from the 54 plants chosen within the two study sites.

A summary of the growth patterns is presented in Table 4. These results are presented as a composite of the three age classes of each species since the data do not indicate that a particular age class would necessarily demonstrate a different growth pattern.

Table 4. Summary of the growth patterns observed in the individual stem joints for the *Opuntia spp.* Increases in weight correlated to increases in stem joint length and decreases in weight correlated to decreases in stem joint length.

Species	Site	% Joints increasing in weight	% Joints with No Net Growth	% Joints decreasing in weignt
O. acanthocarpa	01	52	44	4
	02	39	55	6
O. basilaris	01	17	30	53
	02	50	36	14
O. bigelovii	01	48	34	18
	02	70	26	4

Primary productivity estimates for the three species are presented in Table 5. The results indicate a difference in productivity between the two sites, with the higher elevation site (which receives more rain annually) having yields approximately twice the values of the lower elevation site. The results also indicate the three species possess dissimilar primary productivity yields. At the lower elevation site, the yield for *O. basilaris* is negative, indicating this species has a decreasing biomass. This conclusion is supported by our observations of the population of *O. basilaris* at this site, in as much as the plants do not have unwrinkled pads and few appear to be as vigorous as the plants of the higher elevation site. At both sites the primary productivities for the three species (see Table 5) are significantly lower than the productivity yields of other noncultivated *Opuntia* species (Griffiths, 1915).

Table 5. Estimate of primary productivity for the two study sites. Productivity rates derived from the data summarized in Table 4.

Species	$Kg\ ha^{-1}Yr^{-1}$ Site 01	Site 02
O. acanthocarpa	36.8	50.0
O. basilaris	- 2.8	2.3
O. bigelovii	32.8	68.7

Growth measurements have been recorded for *O. basilaris* and are plotted in Figure 1. The kinetics of growth appear sigmoidal in all cases even though the pads were growing at different rates. Pads A and B were growing on the same plant, which was maintained under cultivated field conditions. Pad C occurred on a plant which was growing in an environmental chamber maintained at near ambient conditions of photoperiod and thermoperiod. The data for Pad D were taken from one of the plants at Deep Canyon (Site 02, Specimen no. 309, Joint no. 1), which was maintained under noncultivated field conditions.

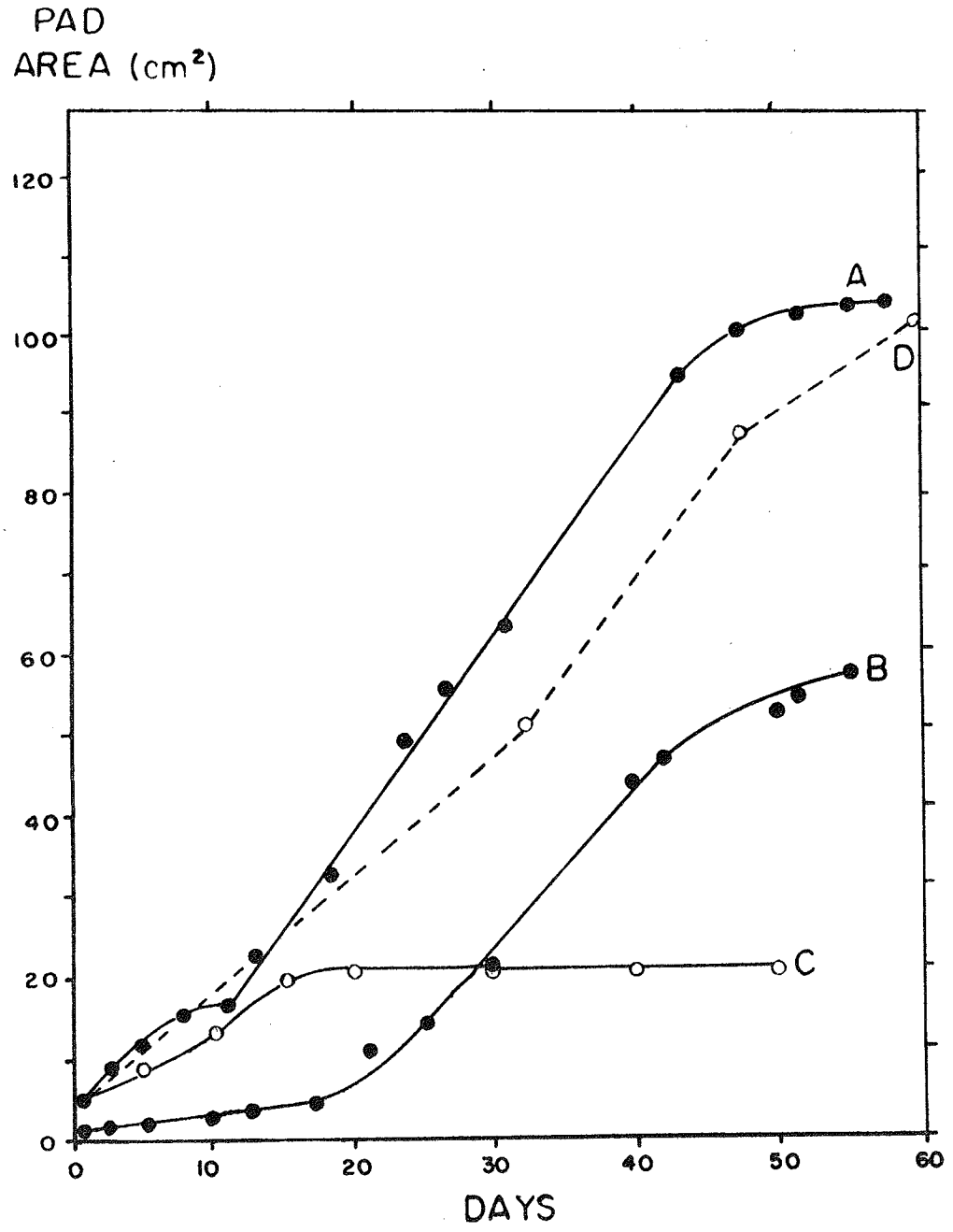

Figure 1. Growth curves for surface area of stem joints of *O. basilaris* as a function of time. Day 0 corresponds to May 8, 1971, for A, B and D, while Day 0 corresponds to July 12, 1971, for C.

Under sustaining field conditions at Deep Canyon, water is certainly a limited environmental factor. In spite of this, Pad D was increasing in dry weight at a rate comparable to Pads A and B, which were receiving excess amounts of water. Assuming its total increase in dry weight comes from fixation of exogenous CO_2 and stomates are open for a daily interval of eight hours, this pad would have a maximum rate of CO_2 assimilation equivalent to 16 mg $CO_2/dm^2/hr$. This estimate is significantly larger than rates of CO_2 assimilation obtained so far under field conditions and suggests the translocation of dry matter into the pad may account for its high rate of dry weight increase.

CO_2 - Assimilation (DSCODE A3UTM20)

The collection of data for field rates of CO_2 assimilation has been restricted to periods following rainfall at Deep Canyon. During the study period there were five separate occurrences of rain at the study sites, and gas exchange by *O. basilaris* has generally been restricted to these same five periods. Attempts to induce measurable rates of gas exchange by irrigating plantsat the scudy sites have been fruitless. Prior to sampling the rates of CO_2 assimilation the relative rates of water vapor exchange were determined with a diffusion resistance hygrometer. Plants having high resistances to water vapor exchange demonstrated low or negligible rates of CO_2 assimilation in all cases. The rates of CO_2 assimilation have been negligible for all samples with *O. basilaris* taken during the daylight hours (even following periods of rainfall). The measurements of CO_2 assimilation available at present are thus restricted to samples taken during the hours of darkness at the two study sites.

The relationship of CO_2 assimilation to the diffusion resistance for CO_2 exchange is presented in Figure 2. The data yield supportive evidence for negligible rates of CO_2 uptake when the diffusion resistance is high. As the diffusion resistance decreases, the rate of CO_2 uptake increases, however, the lowest measured diffusion resistance does not correlate with the maximum rate of CO_2 assimilation for this set of data. In all of the samples the mesophyll resistance to CO_2 diffusion and carboxylation is larger than the associated stomatal and boundary resistances. Significantly lower mesophyll resistances may account for the higher rates of CO_2 assimilation in those pads which have relatively high stomatal and boundary resistances to CO_2 exchange.

The rate of CO_2 assimilation used in Figure 2 has been reported in units of mg $CO_2/dm^2/hr$. The data has also been submitted in units of mg CO_2/mg dry weight of tissue/hr. Plotting the data in terms of the latter units should yield a curve similar to Figure 2 since the relationship between the two forms of the data is nearly linear (Figure 3).

The rates of CO_2 assimilation appear to differ as the length of time following a period of rainfall increases (Figure 4). Given a sufficient amount of water, some of which can be absorbed before the major amount is evaporated out of the soil, the water status of the plant will increase. This type of response may promote gas exchange, and theoretically the greater the amount of water absorbed, the greater the chance of stimulating gas exchange. Rainfall during August 29, 1971, appears to have induced gas exchange by plants of *O. basilaris* during the following two nights. The magnitude of the rates of CO_2 assimilation had increased the second night above the rates of CO_2 assimilation for the first night. The plants sampled during the second night would have had a longer period to absorb available soil water, and this effect might have increased the rates of CO_2 uptake.

The results of the initial work to determine the maximum rate of CO_2 assimilation are presented in Figure 5. The effect of elevated CO_2 concentrations on CO_2 assimilation appears to be linear using concentrations up to 1000 ppm CO_2. Additional experiments will be necessary before the significance of this data can be properly evaluated. Sufficient information is not available at present to determine the maximum CO_2 assimilation rate nor the half-maximum CO_2 concentration, both of which are required for developing a predictive model for estimating productivity.

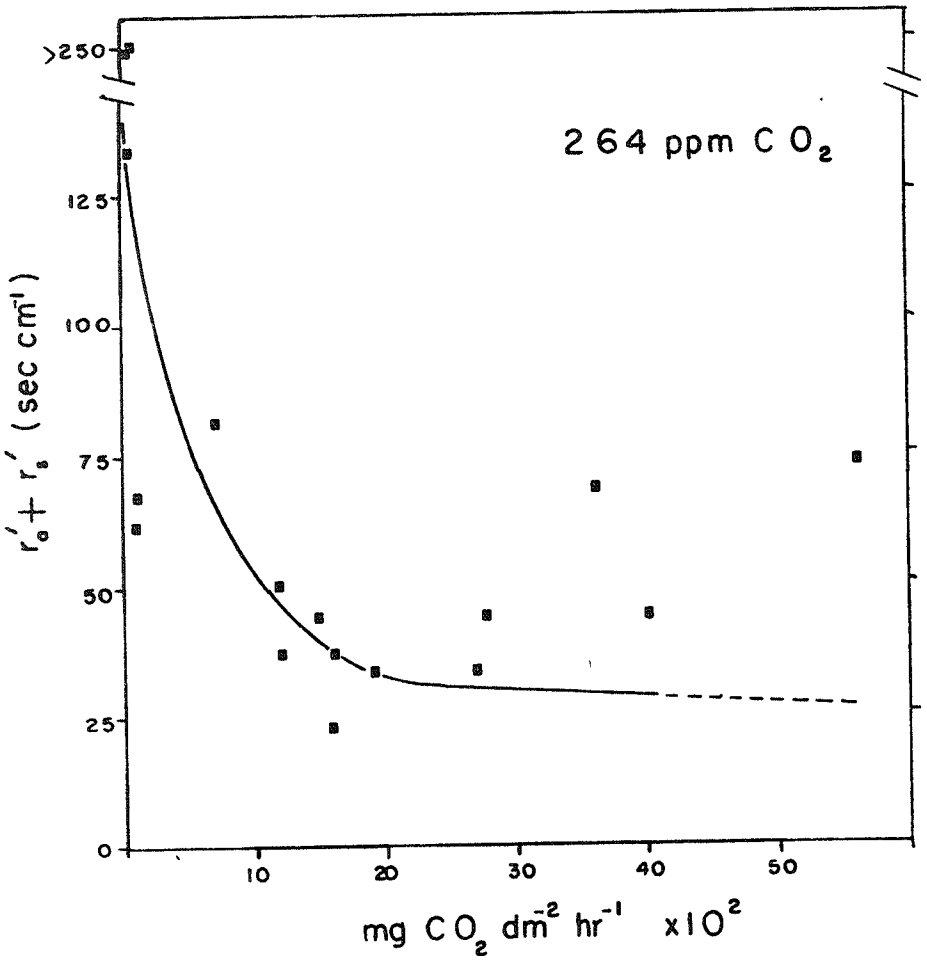

Figure 2. Rates of dark CO_2 fixation in *O. basilaris* as a function of diffusion resistance to CO_2 uptake. Point scatter possibly due to omission of the mesophyll resistance from the total CO_2 diffusion resistance presented.

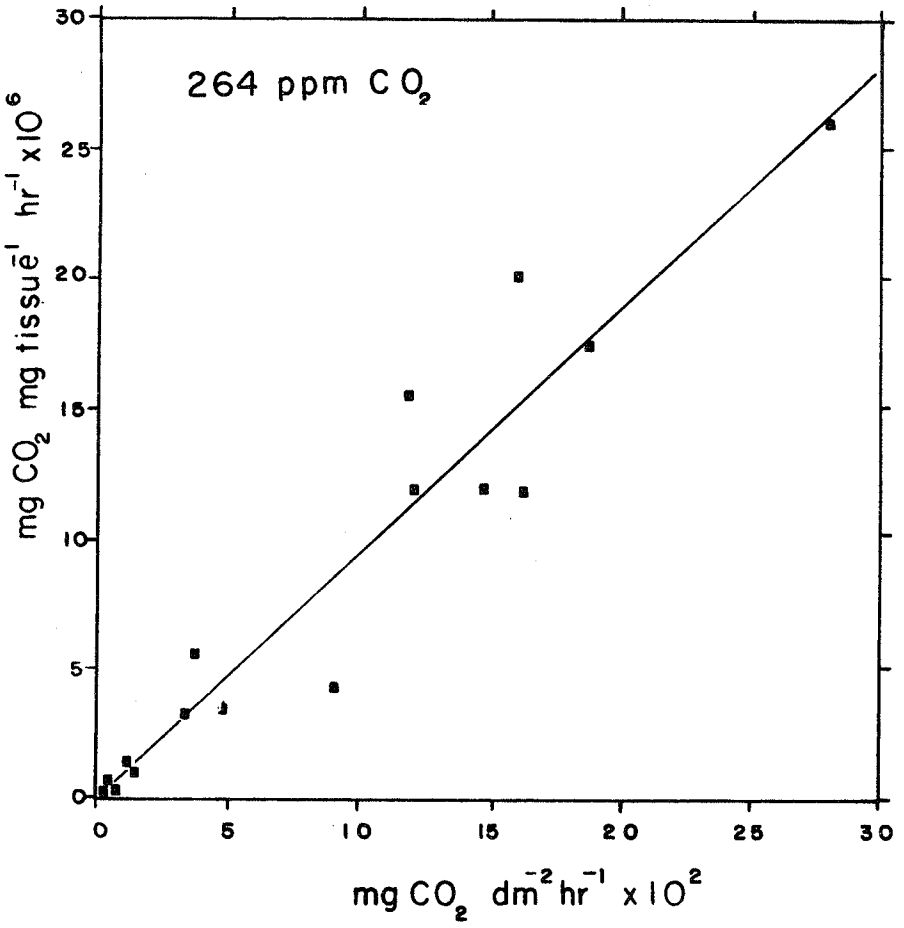

Figure 3. Relationship between rates of CO_2 assimilation based on stem joint surface area and dry weight of tissue for *O. basilaris*.

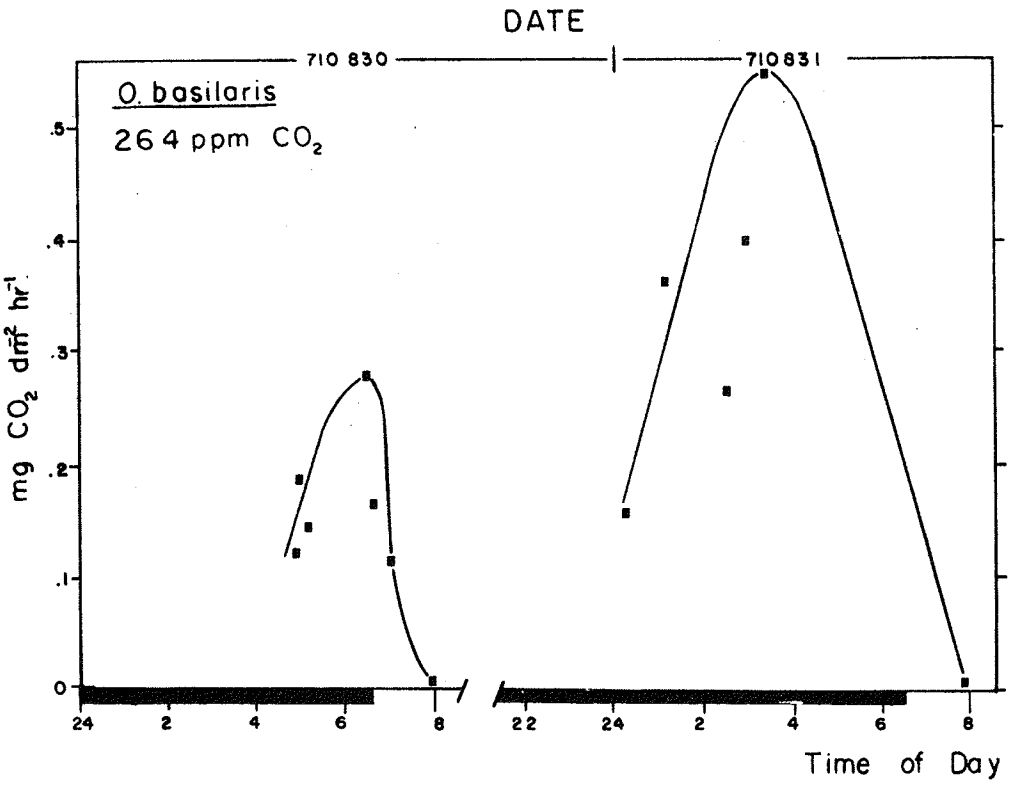

Figure 4. Rates of dark CO_2 fixation in *O. basilaris* as a function of time following rain. Rainfall occurred at 1600 hours during August 29, 1971.

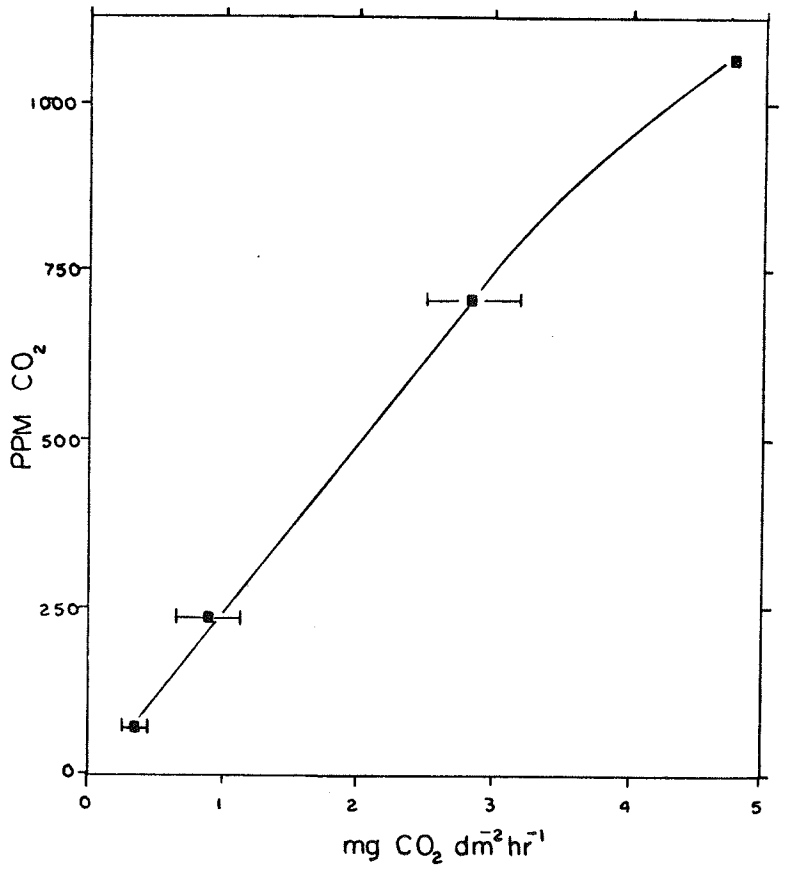

Figure 5. Rates of dark CO_2 fixation in *O. basilaris* as a function of CO_2 concentration. Diffusion resistance values were similar in all stem joints sampled.

Total Acid Number (DSCODE A3UTM21)

Determinations of the total acid content for the three species of *Opuntia* have been conducted. Each species demonstrates a diurnal fluctuation in total acid content, the magnitude of which is different for each species. Typical results for the three species are shown in Figures 6, 7, and 8. Similar diurnal fluctuations in acidity have been demonstrated in other *Opuntia* species (Richards, 1915).

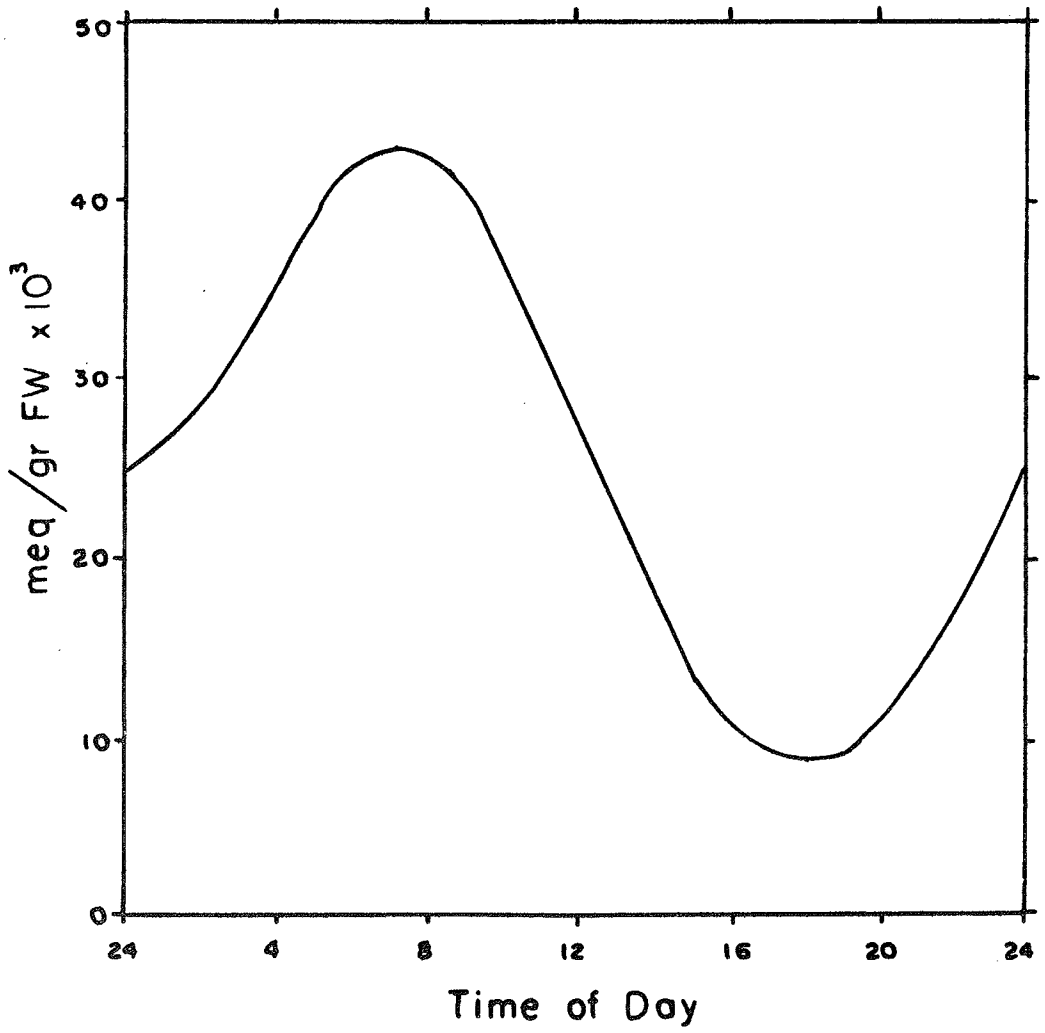

Figure 6. Diurnal fluctuation in total acid content in *O. basilaris* as a function of time. The curve is typical of acid fluctuations throughout the year.

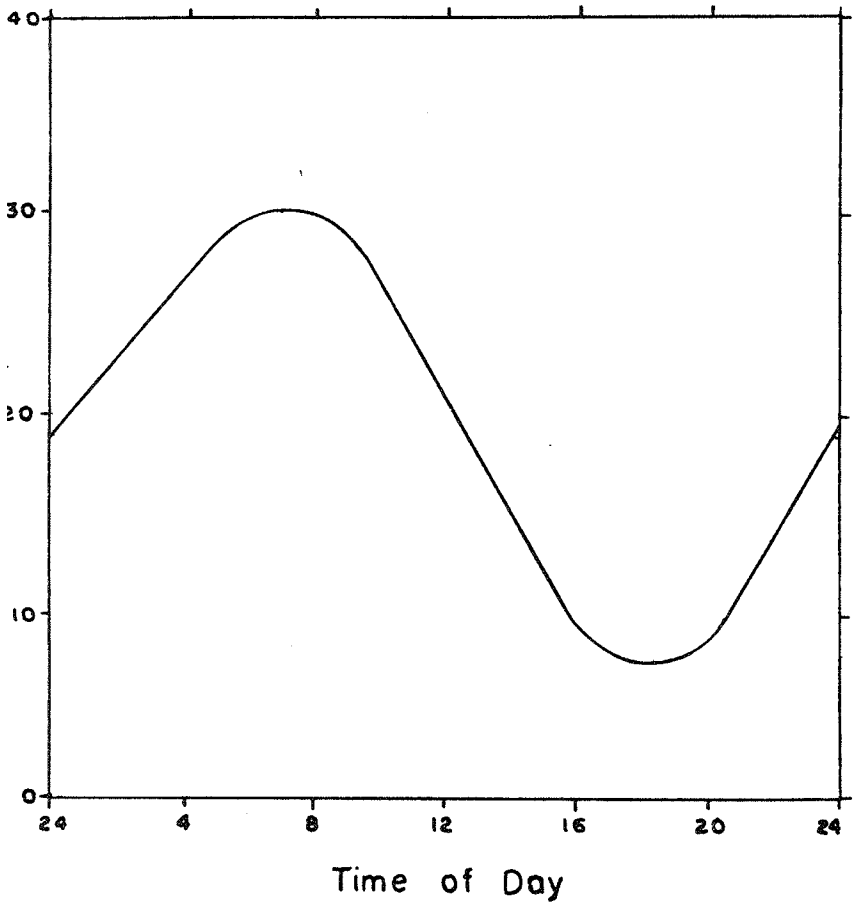

Figure 7. Diurnal fluctuation in total acid content in *O. bigelovii* as a function of time. The curve is typical of acid fluctuations throughout the year.

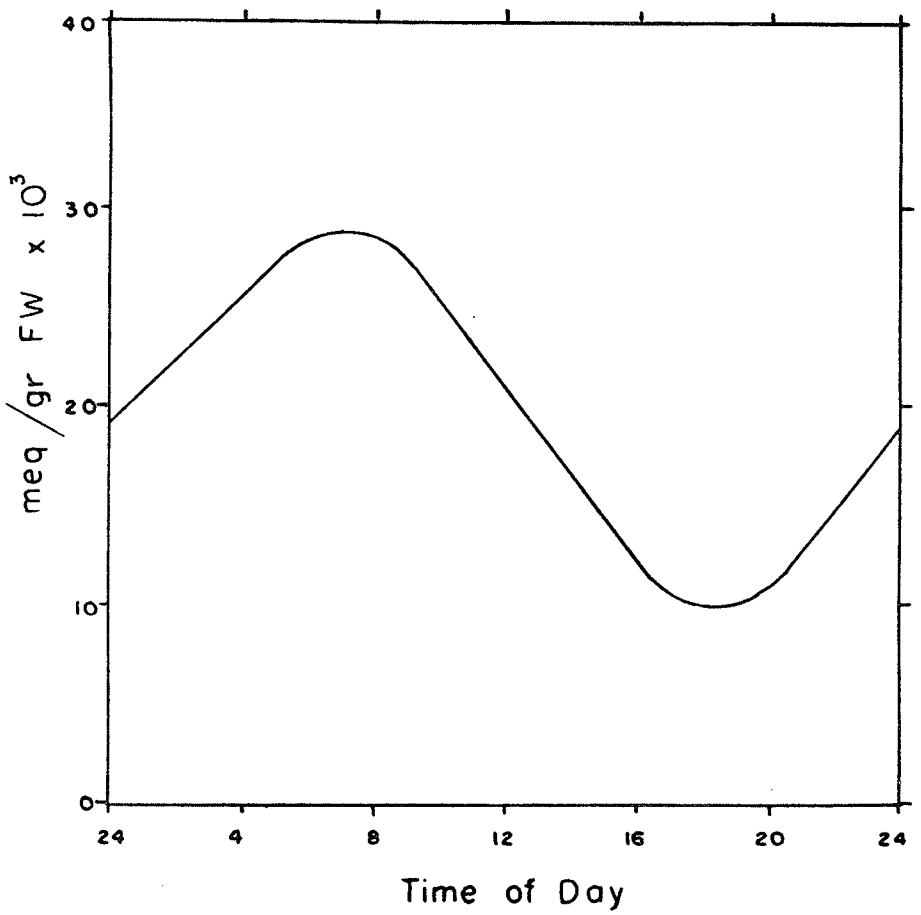

Figure 8. Diurnal fluctuations in total acid content in *O. acanthocarpa* as a function of time. The curve is typical of acid fluctuations throughout the year.

The total acid content has been determined and its fluctuation has been utilized as an indicator of the fluctuation in the free (titratable) acid fraction, since the bound (nontitratable) acid fraction does not fluctuate diurnally (Bennett-Clark, 1933). The fluctuation in total acids has been shown to be due mainly to a fluctuation in malic acid in other CAM species (Pucher et al., 1947), with the other main organic acids showing little diurnal fluctuation. *Opuntia* species are known to demonstrate this type of organic acid metabolism (Ting and Dugger, 1968), and most likely show a similar fluctuation in malic acid.

Under sustaining field conditions, stomates are open in the dark and closed during periods of light. Total exogenous CO_2 fixed is via the dark reactions of CAM and can be estimated by the magnitude of the total acid fluctuation. Coutinho (1965) has shown a perfect correlation with periods of CO_2 fixation and the fluctuation of total acids in *Epidendrum ellipticum*. Theoretically, if all CO_2 released in the light is refixed photosynthetically then the magnitude of photosynthesis can also be estimated by the decrease in total acid content during the light period.

Estimates based on the diurnal fluctuations of total acids are equivalent to dark CO_2 fixation rates of 1.7, 2.8, and 2.2 mg $CO_2/dm^2/hr$ for *O. basilaris*, *O. bigelovii*, and *O. acanthocarpa*, respectively. Previously, we estimated of *Opuntia* species (Ting and Dugger, 1968) that 20% of the dark-fixed CO_2 was not refixed photosynthetically. This loss may occur by dark respiration, photorespiration, or decarboxylation of malate to yield CO_2 which is not refixed in the light. A corrected estimate for photosynthetic carbon assimilation would be 1.4, 2.2, and 1.7 mg $CO_2/dm^2/hr$ for *O. basilaris*, *O. bigelovii* and *O. acanthocarpa*, respectively. In the case of *O. basilaris*, the estimated rate of dark CO_2 fixation is 1 to 1.5 times the measured rate of fixation at ambient concentrations of CO_2.

We feel, however, that a technique can be developed by which photosynthetic carbon assimilation can be estimated in the field by use of the relationship between total acid content and pH. The relationship of such data is relatively good (Figure 9).

Gas Diffusion Resistance and Transpiration (DSCODE A3UTM30)

Gas diffusion resistances have been calculated following calibration of the diffusion resistance hygrometer. The design of the instrument has been repeatedly modified for use with *O. basilaris*, though in its present form it is still unusable on plants of *O. bigelovii* and *O. acanthocarpa*.

The results of our initial work with *O. basilaris* are shown in Figure 10. Additional work has been initiated to develop a family of such curves relating diffusion resistance to calculated rates of transpiration for the variety of possible environmental conditions to which plants of *O. basilaris* are exposed. Attempts to measure transpirational loses in excised stem sections of the other two *Opuntias* have been fruitless.

Water Status Estimates (DSCODE A3UTM40)

Initial attempts to estimate plant water potential by use of a standard curve of relative turgidity have been unrewarding with *Opuntia* tissue below -20 Bars of water potential. Subsequently, the procedure was modified to determine water potential with the use of a thermocuople psychrometer. The results of our earlier work with relative turgidity estimates are shown in Figure 11.

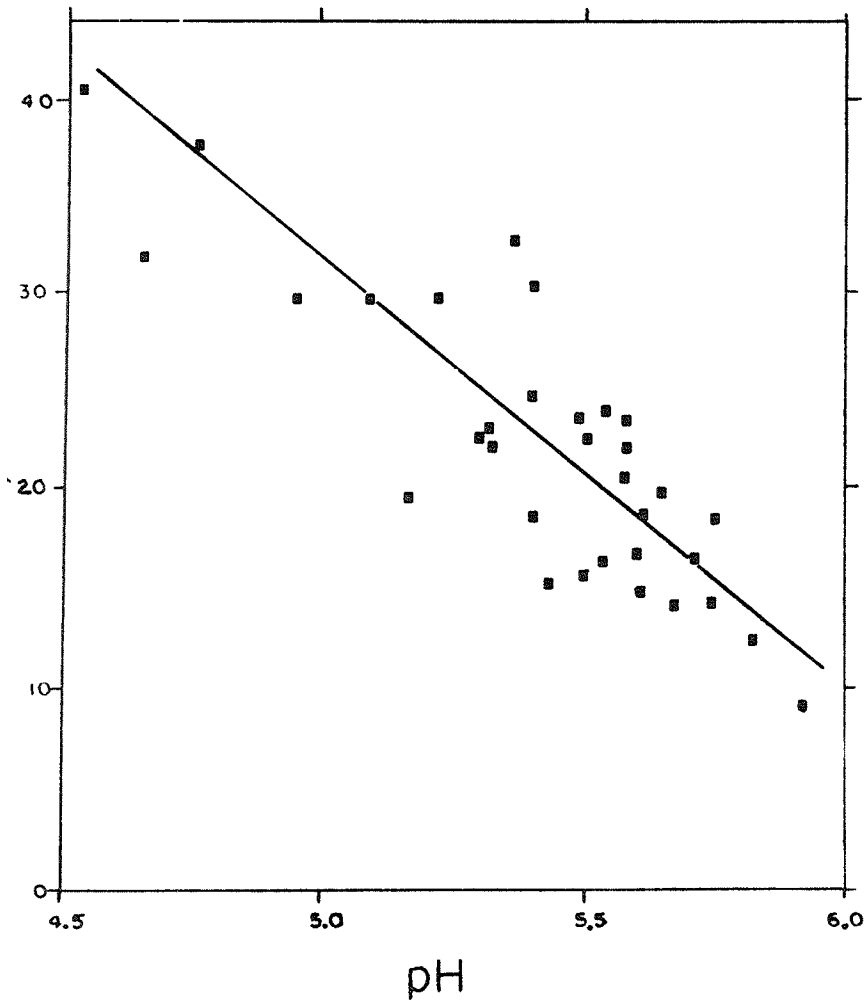

Figure 9. Relationship between pH and total acid content. Data compiled from several samplings with each of the *Opuntia* spp.

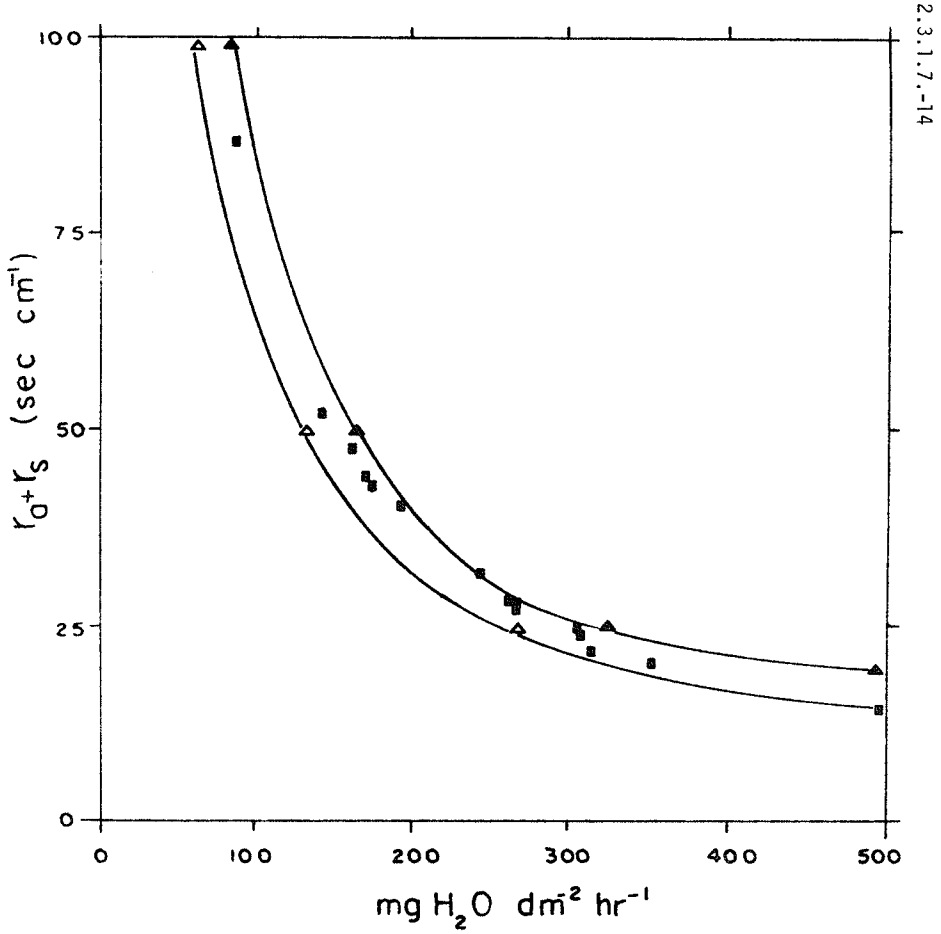

Figure 10. Calculated rates of transpiration in *O. basilaris* as a function of diffusion resistance. Environmental conditions as follows: $t_l \simeq t_a = 26 \pm 1^{o}C$, RH = ± 3%. Theoretical maximum transpiration rates (▲) and minimum transpiration rates (△) presented to show limits under existing environmental conditions.

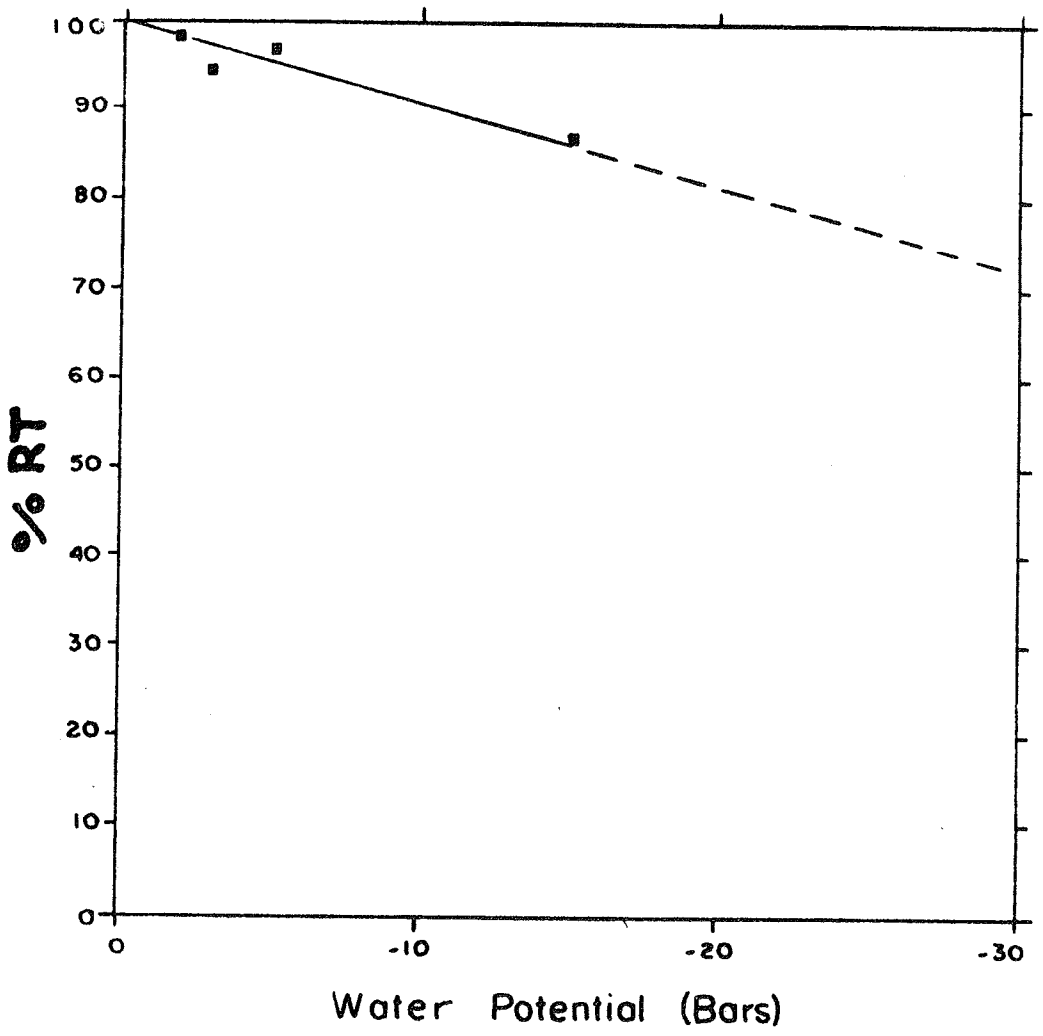

Figure 11. Relationship between tissue water potential in *Opuntia* spp. and relative turgidity of tissue.

The results available at present indicate the *Opuntia* species are able to absorb available soil water and increase their water status within short time periods following rainfall. Absorption of water is more rapid during periods of daylight hours compared with dark absorption rates. Plant water potentials in the *Opuntia* species are relatively uninfluenced by the evaporative demand of the atmosphere, even during periods of available soil water. Under sustaining field conditions stomates are closed during the daylight hours when evaporative demands are highest. The minimum plant water potential levels yet recorded in living stem joints of these *Opuntia* species have been recorded in *O. bigelovii* (ca. -50 Bars). Water potentials in this range have not been found in *O. basilaris* or *O. acanthocarpa*, and we have yet to record an increase in plant water status with soil water potentials in the range of -40 Bars.

The results of irrigating a plant of *O. basilaris* are shown in Figure 12. The plant maintained a high level of water potential after absorption of soil water was completed. This increase in water content reached a maximum level approximately 24 hours following the application of water, though the loss of water vapor was not measurable during the entire periods following irrigation. The results suggest initial stomatal opening (after a period of inactivity) appears to be more controlled by environmental factors, i.e., light and temperature, than by water status.

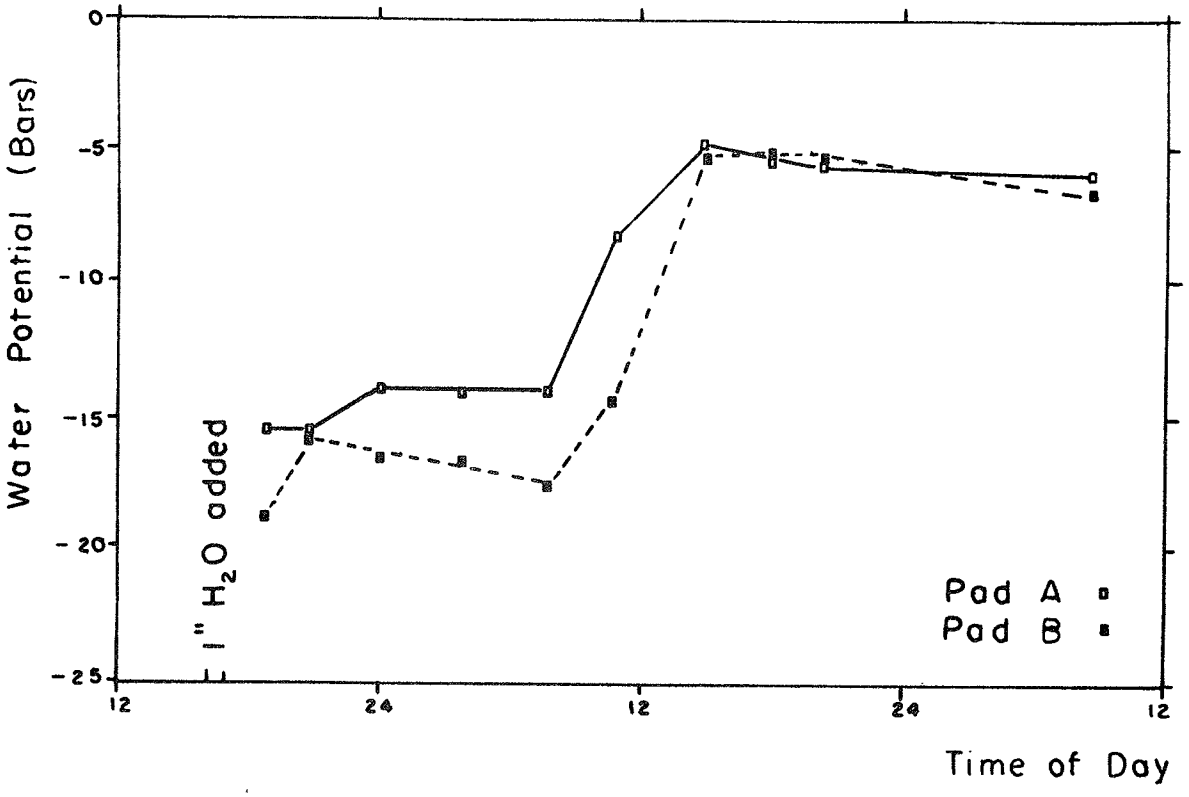

Figure 12. Relationship between tissue water potential in *O. basilaris* as a function of time following irrigation.

Soil Water Status (DSCODE A3UTM60)

Permanent soil psychrometer probes have been placed at the two study sites -- at soil depths of 2 cm, 5 cm, 10 cm, and 15 cm at Site 01, and at soil depths of 2 cm, 10 cm, 15 cm, and 30 cm at Site 02. These soil depths encompass the rooting zones of the three *Opuntia* species. Diurnal profiles of soil temperature and soil water potential have been recorded throughout the study period. In the absence of rain at Deep Canyon, soil water potentials have been below -40 Bars at all soil depths. During periods of soil water potentials below -40 Bars the absorption of soil water and its associated effect on plant water potential has not been detected in the *Opuntia* species.

A typical diurnal profile of soil temperatures during the summer months is shown in Figure 13. Soil temperature fluctuations correlate with fluctuations in air temperature, while the magnitude of the soil temperature fluctuations decreases with increasing soil depths. As the maximum air temperature drops during the winter months the magnitude of the soil temperature fluctuations is further reduced.

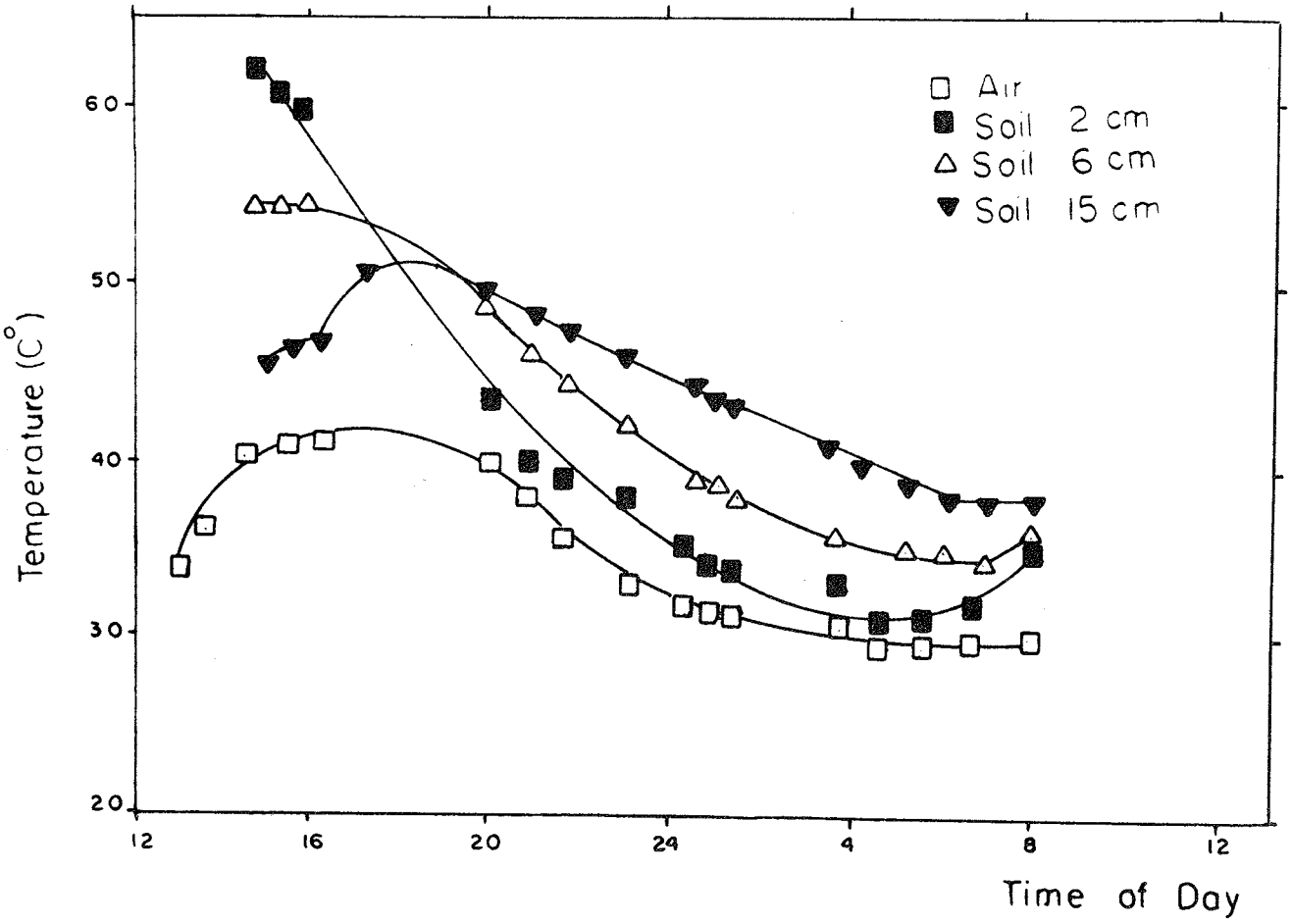

Figure 13. Temperature curves depicting the diurnal fluctuation in temperature at different soil depths and of the air. Recorded during July, 1971.

A summary of the available data on soil water status is shown in Table 6. Deep Canyon characteristically receives most of its rain during the winter months and the two study sites receive different amounts of water during each rainfall. The higher elevation site (Site 02) generally receives more water, averaging 2 to 3 times the amount measured at Site 01. Given larger amounts of rainfall, the moisture penetrates deeper into the soil and takes longer to be evaporated out of the soil. Typically, the evaporative gradient is smaller during the winter months and soil moisture will be removed more slowly than during the summer months. Absorption of soil moisture by the *Opuntia* species is generally restricted to periods following rainfall, which during the winter months would allow a greater amount of absorption than during the summer months. During the summer months the quantity of rainfall has been small and penetration of rain water into the soil is insignificant. Deeper *Opuntia* roots would probably not be absorbing water during the summer months, and those roots nearer the surface would have a limited amount of time to remove available soil moisture. The measurement of gas exchange by plants of *O. basilaris* has been restricted to periods of available soil moisture and the relative rates of CO_2 assimilation have been larger during the winter months than during the summer months.

Table 6. Summary of soil water status data for the two study sites during periods of available soil moisture. Information not available recorded as (--).

Date	Site	Amount of rain (mm)	Maximum Depth of Penetration (cm)	Minimum Soil Water Potential (Bars)	Soil Depth of Minimum Soil Water Potential (cm)	Estimated Time For Soil Water Potential to go Below -40 Bars (Hours)
710721	01	6.8	8	-1	3	30
710829	01	3.0	--	--	--	12
710830	02	3.0	10	-7	10	--
711022	01	25.0	10	-1	2-5	50
711223	01	3.8	5	--	3	--
711223	02	>3.8	15	-3	5	--
711228	01	8.0	20	-1	3-10	150
711228	02	>8.0	30	-1	10	300

DISCUSSION

Differences in standing crop biomass can be attributed to the location of the two study sites in two distinct life zones of vegetation. The lower elevation site (Site 01) is located in a Lower Sonoran life zone and the higher elevation site (Site 02) is located in an Upper Sonoran life zone of vegetation. However, the percent of total biomass contributed by the succulent plants is similar for the two study sites. The dry matter data presently available has a limited utility as the basal and root contributions to total dry matter have yet to be determined. In any case we suspect that the relative contribution of such data will not increase the total dry matter per hectare by more than 40%.

The estimated rates of net primary productivity for the three *Opuntia* species are relatively low. In spite of this fact these plants contain a significant portion of the total net primary production for the desert environment of Deep Canyon. Due to the presence of spines and glochids in the *Opuntia* species, the energy tied up in primary production of these plants is rarely utilized by the large herbivores. The nonsucculent species occurring at Site 02 are generally overgrazed by local populations of desert bighorn sheep (*Ovis canadensis*), which may be a response to the non-palatability of the dominant succulent species. Thus, the general utilization of available net primary production by herbivores is not evident for net primary production of the succulent members of the vegetative community.

Under sustaining conditions at Deep Canyon any dark fixed CO_2 is retained within the plant during the following hours of daylight. The highly impermeable cuticle and the closure of stomata during the hours of daylight aid the retention of CO_2 and water vapor in the *Opuntia* species. Unlike other plants which do not demonstrate CAM activity, the *Opuntia* species do not freely exchange these compounds with the external environment. In spite of their relative low rates of dark CO_2 fixation there is a net assimilation of carbon as respiratory losses of CO_2 do not appear to escape from the impervious stem joints of *Opuntia* species.

During the summer months, gas exchange is restricted to periods following rainfall so that, generally, the plants must survive on the previously fixed CO_2 and absorbed water. The recycling of carbon via a diurnal fluctuation in total organic acids and sugars may be a possible means of transferring reducing power from NAD to NADP (Ting and Dugger, 1965). Since NADPH is utilized in many anabolic pathways, this transfer of chemical energy may constitute an important physiological adaptation which would allow continued synthesis of necessary compounds in the *Opuntia* species during periods of water stress.

Stomatal opening following a period of inactivity would allow loss of water vapor, while initial CO_2 exchange may be limited or not yielding net carbon assimilation. The data suggest that CO_2 fixation varies with the length of time following rain (see Figure 4), with significantly higher rates recorded with longer time periods following available soil moisture. Calculated rates of water-use efficiency also vary with time, the most favorable values recorded the second night (Table 7). While the magnitude of CO_2 uptake increased the second night, the rates of water vapor exchange were similar both nights. The values of water-use efficiency recorded here for *O. basilaris* are significantly lower than the recorded values of other CAM plants (Neales, Patterson and Hartney, 1968).

Table 7. Calculations of water use efficiency (T/P) based on field data obtained with *O. basilaris*.

Date	Time	Transpiration[1]	CO_2 Uptake[2]	T/P
710830	0450	309.3	.120	2577
	0500	353.5	.189	1870
	0510	264.9	.147	1802
	0520	142.5	.090	1587
	0630	264.9	.282	939
	0635	494.6	.162	3053
	0800	231.8	.118	1964
710831	0015	309.2	.160	1932
	0105	169.5	.362	468
	0215	158.7	.566	280
	0228	313.2	.268	1168
	0250	245.8	.401	612

1. units of Mg $H_2O/dm^2/hr$
2. units of Mg $CO_2/dm^2/hr$

During the study period of 1971 we have gained many insights into the response of *Opuntia* species to varying environmental conditions. Numerous questions have developed during the interpretation of the observed responses, many of which have given us further direction in evaluating the interrelationships of gas exchange to varying environmental conditions. Generally, we feel the need to continue collecting field research data, but now on a longer term basis. Field data based on a sequence of a relatively few number of days have a limited applicability in establishing a predictive model which will estimate primary productivity during various environmental conditions.

EXPECTATIONS

During the coming year of the project periodic productivity measurements will continue to be taken and the following new data will be collected:

Biomass

1. Determine the contribution of the subterranean portions of the *Opuntia* species to the total dry matter per hectare.

Carbon dioxide assimilation

1. Field assimilation rates
2. Maximum CO_2 fixation rate
3. Half-maximum CO_2 concentration

Total acid number

1. Investigations of the relationship between total acid number and pH for use in estimating photosynthetic CO_2 assimilation.
2. Significance of internal cycling of CO_2.

Gas diffusion resistance and transpiration

1. Estimates of field transpiration rates occurring in a variety of environmental conditions.
2. Determine minimum diffusion resistances in *O. basilaris*.

Water status estimates

1. Establish a relationship between internal water status and gas diffusion resistances of CO_2 uptake and H_2O vapor loss.

Respiration

1. Estimate rates of respiration for the *Opuntia* species.

Soil water status

1. Establish a relationship between rainfall and length of availability of soil water for absorption by the *Opuntia* species.

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